

# Gastropod Egg Capsules and Their Contents From Deep-Sea Hydrothermal Vent Environments

R. G. GUSTAFSON, D. T. J. LITTLEWOOD, AND R. A. LUTZ

*Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, New Jersey 08903*

**Abstract.** Egg capsules from three different prosobranch gastropods were retrieved from the Galapagos Rift and Juan de Fuca Ridge deep-sea hydrothermal vent fields. The morphology of these capsules and their excapsulated embryos and larvae are described and illustrated. Based on their capsule type and the protoconch morphology of their contained larvae, 29 lenticular capsules from the Galapagos Rift could be attributed to a provisionally described neogastropod turrid, *Phymorhynchus* sp. But 3 inflated, triangular capsules from the Galapagos Rift, and 56 different egg capsules from the Juan de Fuca Ridge, each shaped like an inflated pouch, could not be unambiguously assigned to a member of the known vent gastropod fauna. The mode of development and potential for dispersal is inferred from egg capsule type, the number of embryos per capsule, and protoconch characters comparable to those of confamilial shallow-water gastropods for which the type of development is known. These criteria and a comparison to the known juvenile shell morphology of *Phymorhynchus* sp., suggest that, after encapsulation, this species develops planktotrophically and is capable of long-range dispersal. Similar evidence suggests that the larvae contained in the inflated triangular capsules from the Galapagos Rift may also develop planktotrophically after hatching; but the larvae in the pouch-like egg capsules from the Juan de Fuca Ridge probably develop non-planktotrophically without a dispersal stage. These developmental patterns are characteristic of shallow-water members of the systematic groups to which these species belong, indicating, as previous studies have shown, that vent gastropods can persist in these patchy, ephemeral environments in the absence of unique adaptations allowing dispersal between active hydrothermal sites.

## Introduction

Active hydrothermal vent systems accompanied by dense benthic fauna occur at several widely separated sites along active oceanic ridges in the eastern Pacific, from 48°N along the Juan de Fuca Ridge, to 22°S along the East Pacific Rise. Known hydrothermal fields on the Juan de Fuca Ridge are separated by as much as 100 km, whereas separation along transform faults on the East Pacific Rise indicates that vent fields are at least 100 km apart in this region (Crane, 1985; Grassle, 1986). Local vent habitats appear to be transient, with populations being susceptible to intermittent establishment and extinction (Lutz *et al.*, 1985; J. F. Grassle, 1985; Lutz, 1988). Despite their apparent geographic isolation and ephemeral nature, vent areas are characterized by the remarkable similarity of their faunal assemblages (Lutz, 1988). Fundamental biological questions remain regarding both the manner in which these ephemeral habitats are colonized, and the mechanisms of organism dispersal and rates of gene flow between discrete areas of hydrothermal activity associated with contiguous and non-contiguous oceanic ridge systems.

Because laboratory culture of deep-sea organisms is difficult (Turner *et al.*, 1985), many of our perceptions about the development and larval dispersal of vent biota have been, by necessity, inferred from analyses of egg size, fecundity, and morphology of larval structures retained on juvenile and adult specimens. Gastropod mollusks have been widely used for such studies, because a record of the larval developmental pattern can be inferred from the morphology of the initial shell, comprising the Protoconch I in non-planktrophic species and, also, the Protoconch II shell stages, in planktrophic species (Powell, 1942; Thorson, 1950; Shuto, 1974; Robertson, 1976; Jablonski and Lutz, 1980).

The mode of larval development in recent (Rodriguez Babio and Thiriot-Quiévreux, 1974; Bandel, 1975a, b, c,

1982; Bouchet, 1976a, b; Scheltema, 1978; Bouchet and Warén, 1979b; Rex and Warén, 1982; Scheltema and Williams, 1983; Lutz *et al.*, 1984, 1986; Turner and Lutz, 1984; Turner *et al.*, 1985; Colman *et al.*, 1986; Lutz, 1988; Lima and Lutz, 1990) and fossil (Jung, 1975; Scheltema, 1978, 1981; Jablonski and Lutz, 1980, 1983; Bouchet, 1981; Hansen, 1982, 1983; Jablonski, 1986) prosobranch gastropods has been classified as either planktotrophic or non-planktotrophic based on criteria of larval shell morphology formulated by Kesteven (1912), Dall (1924), Powell (1942), Thorson (1950), Robertson (1971, 1976), Rodriguez Babio and Thiriou-Quévieux (1974), Shuto (1974), Sohl (1977), and Jablonski and Lutz (1980, 1983).

Prosobranch species with larval shells having 1.5 to 9 whorls, a distinct fine sculpture, a brown coloration in contrast to a white or gray adult shell, a narrow high spire, a clear difference between the Protoconch I and Protoconch II, and possibly a projection on the outer lip of the larval shell which interdigitates with the velum [“sinu-sigera” larvae in terminology of Robertson (1976)] are categorized as planktotrophic. Species with larval shells having 0.5 to 1.5 whorls, simple or no ornamentation, the same coloration as the teleoconch, a large bulbous apex, and no evidence of separation between the Protoconch I and Protoconch II are categorized as non-planktotrophic. In the general terminology of Thorson’s (1950) “apex theory,” shells of the planktotrophic type are termed multispiral or polygyrate and shells of the non-planktotrophic type are termed paucispiral.

Although these criteria allow differentiation between planktotrophic and non-planktotrophic larvae, recent culturing of trochoidean archeogastropods demonstrates that the presence of a paucispiral protoconch is insufficient evidence on which to discriminate between a planktonic and a non-planktonic larval existence (Hadfield and Strathmann, 1990). Of four trochoideans cultured, Hadfield and Strathmann (1990) found two with pelagic development of 7 d or more and two with entirely benthic life histories, although all four produced veliger larvae and had similar inflated paucispiral protoconchs. Although the mode of larval development in shelled opisthobranchs may also be reflected in the larval shell morphology, this relationship has not been demonstrated throughout the group (Rex and Warén, 1982).

Ockelmann (1965) formulated criteria distinguishing between planktotrophic and non-planktotrophic development in a wide range of bivalves based on relatively precise dimensions of the prodissoconch I and II, but the only effort to establish similar criteria for gastropod protoconchs was based on data from comparatively few species (Lima and Lutz, 1990). Nevertheless, Shuto (1974) has shown that, given a complete Protoconch I and II, the ratio of the maximum diameter (D; in mm) of the whole protoconch to the number of whorls or volutions

(Vol) provides an index to the developmental type of a marine prosobranch gastropod. A species with more than three whorls and a D/Vol value less than 0.3 suggests planktotrophic development. A D/Vol value between 0.3 and 1.0 with less than three volutions indicates a species with either planktotrophic or non-planktotrophic development, whereas a D/Vol value between 0.3 and 1.0 and less than 2.25 volutions suggests a species with a non-planktotrophic larval type. A D/Vol value higher than 1.0 would suggest a species with direct development (Shuto, 1974). However, Pawlik *et al.* (1988) have shown that the criteria of Shuto (1974) cannot accurately predict the actual mode of development in a majority of cancellariid gastropods.

The type of sculpture or ornamentation on the protoconch has been widely used to infer the mode of development in prosobranch gastropods (Thorson, 1950; Shuto, 1974; Bandel, 1975a, b, c, 1982; Lima and Lutz, 1990). Planktotrophy has been indicated for those larvae with protoconchs possessing a fine reticulate or cancellate pattern, oblique radial ribs or both, whereas a smooth or simply sculptured protoconch suggests that the larvae are non-planktotrophic (Thorson, 1950; Shuto, 1974; Bandel, 1975a, b, c, 1982). A well developed protoconch ornamentation is thought to strengthen the shell, a benefit to planktotrophic larvae spending lengthy periods in the plankton (Bandel, 1975a; Jablonski and Lutz, 1980). Two recent reviews of poecilogony, or intraspecific variation in the mode of larval development, found no evidence for the occurrence of this phenomenon in prosobranch gastropods, indicating that the form of the protoconch is a species-specific character (Hoagland and Robertson, 1988; Bouchet, 1989). Nevertheless, the species variability of protoconch and teleoconch morphologies of cultured meso- and neogastropods led Lima and Lutz (1990) to stress the need for caution when inferring type of development from shell morphology alone.

The most reliable method for determining developmental mode from protoconch morphologies is to compare confamilial or congeneric species with known developmental histories (Scheltema, 1978; Jablonski and Lutz, 1980, 1983). In the case of deep-sea prosobranchs, the comparison must be made with taxonomically related shallow-water species, the assumption being that similar protoconch morphologies result from similar life history patterns in shallow and deep seas (Colman *et al.*, 1986).

Based on the above larval shell criteria, the majority of vent gastropods are believed to have non-planktotrophic development and to have limited larval dispersal capability (Lutz *et al.*, 1984, 1986; Turner *et al.*, 1985), although low temperatures encountered in the deep sea may extend the period available for dispersal of swimming but non-feeding veligers (Turner *et al.*, 1985). This abundance of non-planktotrophy may, in part, be due to the fact that

Table I

DSV "Alvin" dive number, date, location, latitude/longitude, and depth of dives in which gastropod egg capsules were retrieved

Dive #	Date	Location	Latitude; Longitude	Depth (m)
1418	24 July 1984	Juan de Fuca Ridge Endeavour Segment	47°57.0'N; 129°04.0'W	2212
1419	25 July 1984	Juan de Fuca Ridge Endeavour Segment	47°57.0'N; 129°04.0'W	2208
1523	11 March 1985	Galapagos Rift Rose Garden Vent	0°48.3'N; 86°13.5'W	2450
1527	16 March 1985	Galapagos Rift Rose Garden Vent	0°48.3'N; 86°13.5'W	2450
1528	17 March 1985	Galapagos Rift Rose Garden Vent	0°48.3'N; 86°13.5'W	2450
1529	18 March 1985	Galapagos Rift Rose Garden Vent	0°48.3'N; 86°13.5'W	2450
1531	20 March 1985	Galapagos Rift Rose Garden Vent	0°48.3'N; 86°13.5'W	2450
2031	3 May 1988	Galapagos Rift Rose Garden Vent	0°48.3'N; 86°13.5'W	2450

the majority of gastropods found at the vents are limpet-like or coiled archeogastropods. When found in shallow seas, these gastropods appear to be phylogenetically constrained to non-planktotrophy (Anderson, 1960; Heslinga, 1981; Strathmann, 1978a, b; Rex and Warén, 1982; Lutz *et al.*, 1984; Jablonski, 1985; Warén and Bouchet, 1989).

Analysis of developmental stages contained in benthic egg capsules also provides information about the life history of bottom-dwelling gastropods. Although many researchers have described the egg capsules and encapsulated embryos of shallow-water (see reviews in Fretter and Graham, 1962; Robertson, 1976; Webber, 1977; Fretter, 1984; Pechenik, 1986; Soliman, 1987; M. F. Strathmann, 1987) and deep-sea (Thorson, 1940b; Bouchet and Warén, 1979a, 1980, 1985a, 1985b; Colman and Tyler, 1988) marine prosobranch gastropods, only brief mention has been made of the rarely collected egg capsules from hydrothermal vent habitats and their contents (Turner *et al.*, 1985; Berg, 1985). "Lens-shaped" egg capsules measuring 10–12 mm (Turner *et al.*, 1985) or  $17.7 \pm 3.8$  mm (Berg, 1985) in diameter have been reported at the Galapagos Rift, while Berg (1985) has briefly described four small prosobranch egg capsules 4.9 mm in length by 1.7 mm wide and shaped like an "inflated triangle" from Garden of Eden vent on the Galapagos Rift.

When specimens of the previously reported egg capsules from the Galapagos Rift (Turner *et al.*, 1985; Berg, 1985) and numerous egg capsules from the Endeavour Segment of the Juan de Fuca Ridge, came into our possession, it was evident that a more detailed study of these capsules and their contents might yield insights into the life histories and the means of dispersal of these species. This paper is a description of the morphology of three different egg capsules from hydrothermal vents and the embryos

and larvae contained in those capsules. Inferences are also made about the dispersal capabilities of the contained larvae, and an attempt is made to predict which of the known hydrothermal vent gastropod species produced each capsule type.

#### Materials and Methods

Specimens were retrieved with the assistance of DSV "Alvin" during the dives summarized in Table I. Egg capsules were collected: (1) from the surfaces of geological and biological samples brought up in the "Alvin" basket or in insulated retrieval boxes; (2) from sampling gear or markers that had been left at the vents and later retrieved; and (3) from sorted material collected with a "slurp gun" attached to "Alvin."

On board ship, specimens were fixed for 24–48 h in 10% formalin buffered with borax, thoroughly rinsed, transferred to 70% ethanol, and finally to 95% ethanol to prevent corrosion of larval protoconchs. Terminology used in egg capsule descriptions follows that of D'Asaro (1970a). Egg capsule length is the distance between the lateral edges at the widest point parallel to the apical suture; width is the distance between the two sides at the widest point perpendicular to the apical suture; and height is the distance from the apex to the basal membrane through the capsule's central axis.

Photographs, drawings, and measurements were made of pertinent views of the capsules. Capsules containing embryos were then dissected into two equal halves and the embryos were removed. Both capsules and free embryos were critical point dried, placed on stubs, coated with approximately 400 Å of gold-palladium, and examined on an Hitachi S-450 scanning electron microscope (SEM).

Table II

Average dimensions (mean  $\pm$  standard deviation) of hydrothermal vent gastropod egg capsules collected on specific dives of DSV "Alvin". Number of specimens collected on each dive are in parentheses

Galapagos Rift Lenticular Egg Capsules			
"Alvin" Dive #	Length (mm)	Width (mm)	Height (mm)
1528 (2)	14.9 $\pm$ 0.8	13.4 $\pm$ 0.0	—
1529 (1)	17.4	15.9	—
1531 (4)	16.4 $\pm$ 1.3	14.0 $\pm$ 0.7	—
2031 (22)	14.4 $\pm$ 1.7	13.9 $\pm$ 1.8	—
Galapagos Rift Inflated-Triangular Egg Capsules			
"Alvin" Dive #	Length (mm)	Width (mm)	Height (mm)
1523 (1)	4.1	1.1	2.4
1527 (1)	3.2	1.1	3.2
1528 (1)	5.0	1.6	3.4
Juan de Fuca Ridge Egg Capsules			
"Alvin" Dive #	Length (mm)	Width (mm)	Height (mm)
1418 (8)	3.3 $\pm$ 0.6	1.2 $\pm$ 0.1	2.7 $\pm$ 0.7
1419 (48)	3.7 $\pm$ 0.5	1.4 $\pm$ 0.3	3.8 $\pm$ 0.6

Values for the maximum dimension of the protoconch and the number of volutions of the larval shell were measured directly from scanning electron micrographs by the methods of Shuto (1974). Maximum diameter of the protoconch was defined as the straight-line distance from the protoconch-teleoconch boundary to the opposite side of the protoconch in the region of greatest width. Maximum diameter of the Protoconch I was defined as (1) the greatest

straight-line distance from the Protoconch I-Protoconch II boundary in species with planktotrophic development, or (2) from the Protoconch I-teleoconch boundary in non-planktotrophic species lacking a Protoconch II, to the opposite side of the Protoconch I in the region of greatest width [see Lima and Lutz (1990), their figure 1B, for a diagrammatic depiction of these dimensions]. Maximum diameter measurements of the protoconch should not be confused with Robertson's (1971) "first whorl diameter," which is a measurement of the straight-line distance tangent to the straight beginning of the suture and extended in both directions to where it intersects the nearest suture (Lima and Lutz, 1990, their figure 1A). All these values are most accurately determined when the shell is viewed with an apical orientation. Taxonomic terminology and categories are in agreement with those outlined in Vaught (1989).

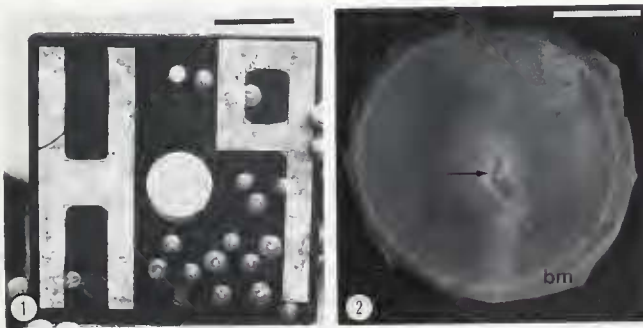
## Results

The gastropod egg capsules described in this report consist of three distinct groups: (1) lenticular capsules, with a flattened oval or circular base and a convex upper surface, from the Galapagos Rift; (2) inflated triangular-shaped capsules, from the Galapagos Rift; and (3) inflated oval or pouch-like capsules attached to the substratum by a flattened basal membrane, from the Endeavour Segment of the Juan de Fuca Ridge. Dimensions of each collected capsule are summarized in Table II.

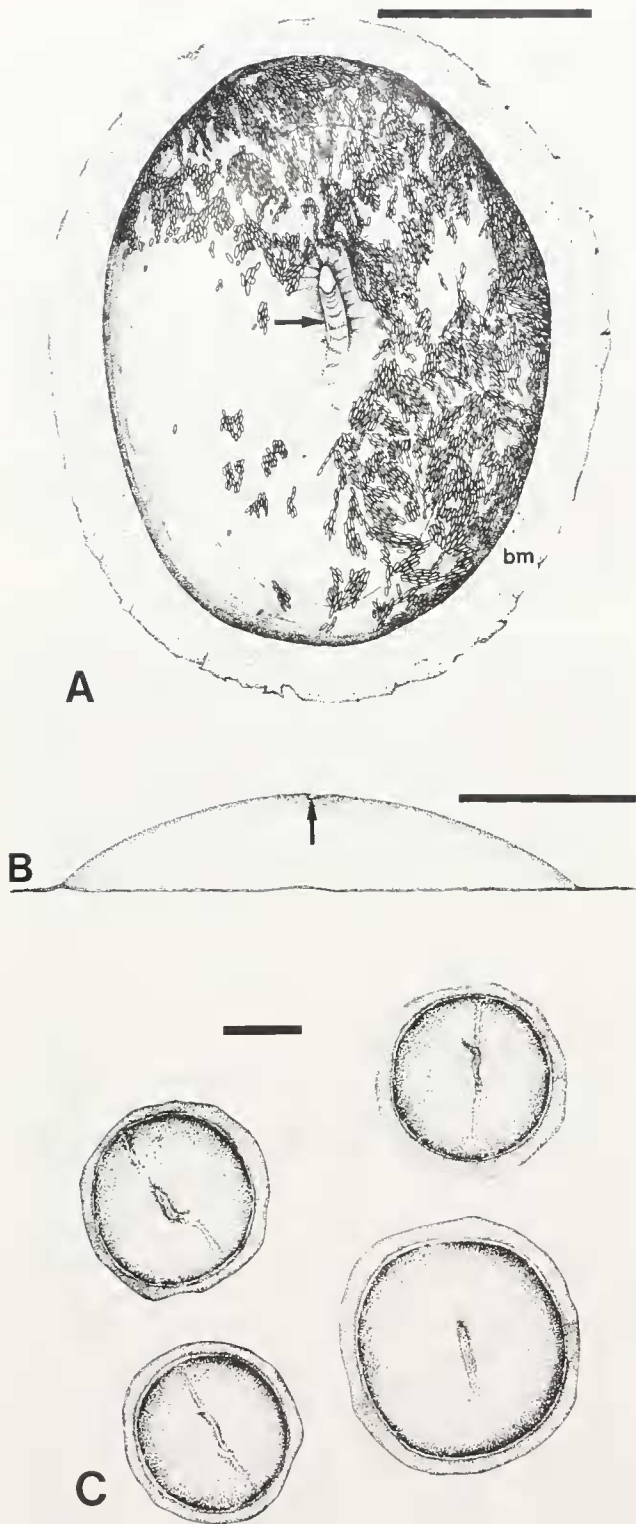
### Galapagos Rift lenticular egg capsules

Twenty-nine round to oval, lenticular egg capsules averaging  $14.8 \pm 1.8$  mm in length by  $14.0 \pm 1.7$  mm in width were collected during four separate dives at Rose Garden Vent on the Galapagos Rift (Figs. 1–3; Tables I, II). Height could not be measured due to unequal deformation of the capsules during fixation and dehydration. Twenty-two capsules were found attached to a gray polyethylene marker retrieved on "Alvin" Dive 2031 (Fig. 2), while the remaining specimens were found attached to basaltic rocks by a thin basal membrane that extends beyond the limits of the capsule chamber (Figs. 2, 3).

The outer surface of the whitish to transparent capsules was smooth; there were no apparent ridges (Figs. 2, 3). A transparent elongated escape aperture, centered about the long axis of each capsule, blended into an indistinct apical suture that effectively separated each low capsule into two equal halves (Figs. 2, 3). The capsule wall had three layers consisting of a compact, dense inner layer, a spongy-fibrous middle layer, and a compact, dense outer layer. (Figs. 4–5). The elongated escape aperture was derived from a hollow chamber within the middle spongy-fibrous layer; this chamber caused the capsule wall to bulge outward above the level of the capsule surface (Fig. 5).



Figures 1–2. Lenticular egg capsules from Rose Garden Vent on the Galapagos Rift. Figure 1. Photograph of egg capsules attached to location marker retrieved on "Alvin" Dive 2031. Scale bar = 50 mm. Figure 2. Light micrograph of apical view of egg capsule removed from substrate. Arrow marks the escape aperture. Scale bar = 5 mm. bm, basal membrane.



**Figure 3.** (A) Apical view of lenticular egg capsule from the Galapagos Rift with individual embryos visible through transparent capsule wall. Arrow marks the escape aperture. Scale bar = 5 mm. bm, basal membrane. (B) Lateral view of lenticular egg capsule with peripheral extension of basal membrane. Arrow marks the escape aperture. Scale bar = 5 mm. (C) Group of four lenticular capsules drawn as they appeared attached to location marker in Figure 1, prior to fixation. Scale bar = 5 mm.

Early trochophore and veliger larvae in various stages of development were present in capsules collected during "Alvin" Dives 1528, 1529, and 1531 (Figs. 6–11); one capsule collected during Dive 2031 contained 1052 veliger larvae, all with a fully formed Protoconch I (Figs. 12–14). All other lenticular capsules collected during Dive 2031 were empty. No nurse eggs were observed in lenticular egg capsules.

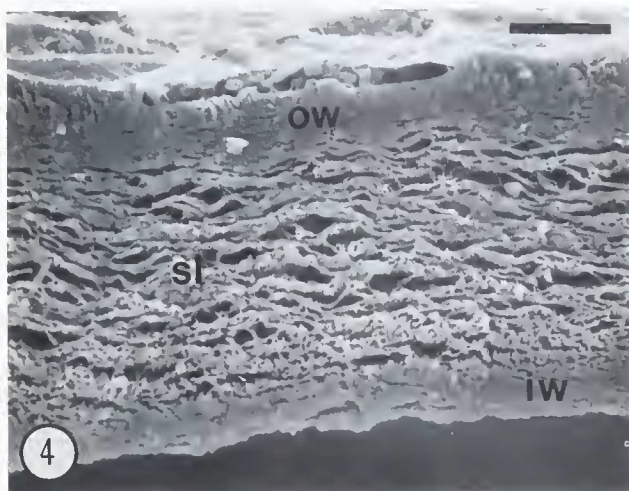
The following is a chronological reconstruction of developmental stages found in a number of lenticular capsules from the Galapagos Rift. The earliest stage encountered, a late prototroch, was approximately 175  $\mu\text{m}$  in length by 100  $\mu\text{m}$  in width (as measured from electron micrographs), with a prominent apical plate, short pre-trochal region, prototroch, long post-trochal region, mouth, and very early larval shell (Figs. 6–10). The apical plate lacked an apical ciliary tuft while the prototrochal cilia appeared to be of the compound type and 15–19  $\mu\text{m}$  in length (Fig. 7). The posterior-dorsal shell field (see Eyster and Morse, 1984, for terminology) had already invaginated in the earliest specimens obtained, and some shell secretion had commenced (Figs. 8–10).

The next observed stage of development was a veliger larva, which had a bi-lobed velum, a mouth leading into the stomadeum, a foot primordium—a protruding knob located immediately posterior to the mouth—an operculum, and a more developed larval shell (Fig. 11). This was a very early veliger because the body was still much too large to be withdrawn into the shell.

One capsule collected during Dive 2031 (Figs. 12–14) contained late Protoconch I larvae that were almost ready to hatch. The embryonic shells of these specimens had a maximum diameter of 234  $\mu\text{m}$  (as measured from electron micrographs). The larval shells of these larvae had a fine reticulate sculpture formed of spiral raised ridges running in the direction of growth, and crossed by regularly spaced perpendicular riblets (Figs. 12–14). An uncalcified operculum was present at this stage (Fig. 13).

#### *Galapagos Rift inflated triangular egg capsules*

Three specimens of an egg capsule  $4.1 \pm 0.9$  mm in length by  $1.3 \pm 0.3$  mm in width by  $3.0 \pm 0.5$  mm in height and shaped like an inflated triangle were found attached to basaltic substrates during a series of "Alvin" dives at the Galapagos Rift in 1985 (Figs. 15, 16; Table II). Capsules were attached by a basal membrane that barely extends beyond the limits of the capsule chamber (Fig. 16). A lateral ridge extended up from either end of the long axis of these capsules to meet at the capsule's slightly off-center apex (Figs. 15, 16). Except for the prominent lateral ridge, the surfaces of these capsules were smooth. Capsules fixed in 10% buffered formalin and subsequently stored in ethanol, ranged in color from white



Figures 4–5. Scanning electron micrographs of lenticular egg capsule wall from Galapagos Rift. **Figure 4.** Cross-section of capsule wall. Scale bar = 10  $\mu\text{m}$ . ow, outer capsule wall; sl, spongy layer. **Figure 5.** Cross-section through the escape aperture chamber. The outer surface of the capsule is towards the top. Scale bar = 100  $\mu\text{m}$ .

to yellowish-white to almost orange. The capsule wall was composed of what appeared to be one spongy-fibrous layer (Fig. 17).

Each capsule contained several hundred early veliger larvae approximately 165  $\mu\text{m}$  in length by 98  $\mu\text{m}$  in width, as measured from electron micrographs. Larvae in all three capsules were at the same relative stage of development and were characterized by a bi-lobed velum, an apical sensory region with cephalic cilia, a mouth, a foot primordium with attached operculum, and an early Protoconch I (Figs. 18, 19). Velar compound cilia were approximately 30  $\mu\text{m}$  long. The early protoconch was overlaid by a membrane that obscured a sculpture of radially arranged rows of short tubercles intersected by weak concentric raised ridges or lines (Figs. 19–21). Distal to this membrane, the sculpture consisted of parallel raised ridges running in the direction of growth, crossed by radial riblets, and forming a cancellate or net-like pattern (Fig. 19). Nurse eggs were not present in the three inflated triangular egg capsules.

#### *Juan de Fuca Ridge egg capsules*

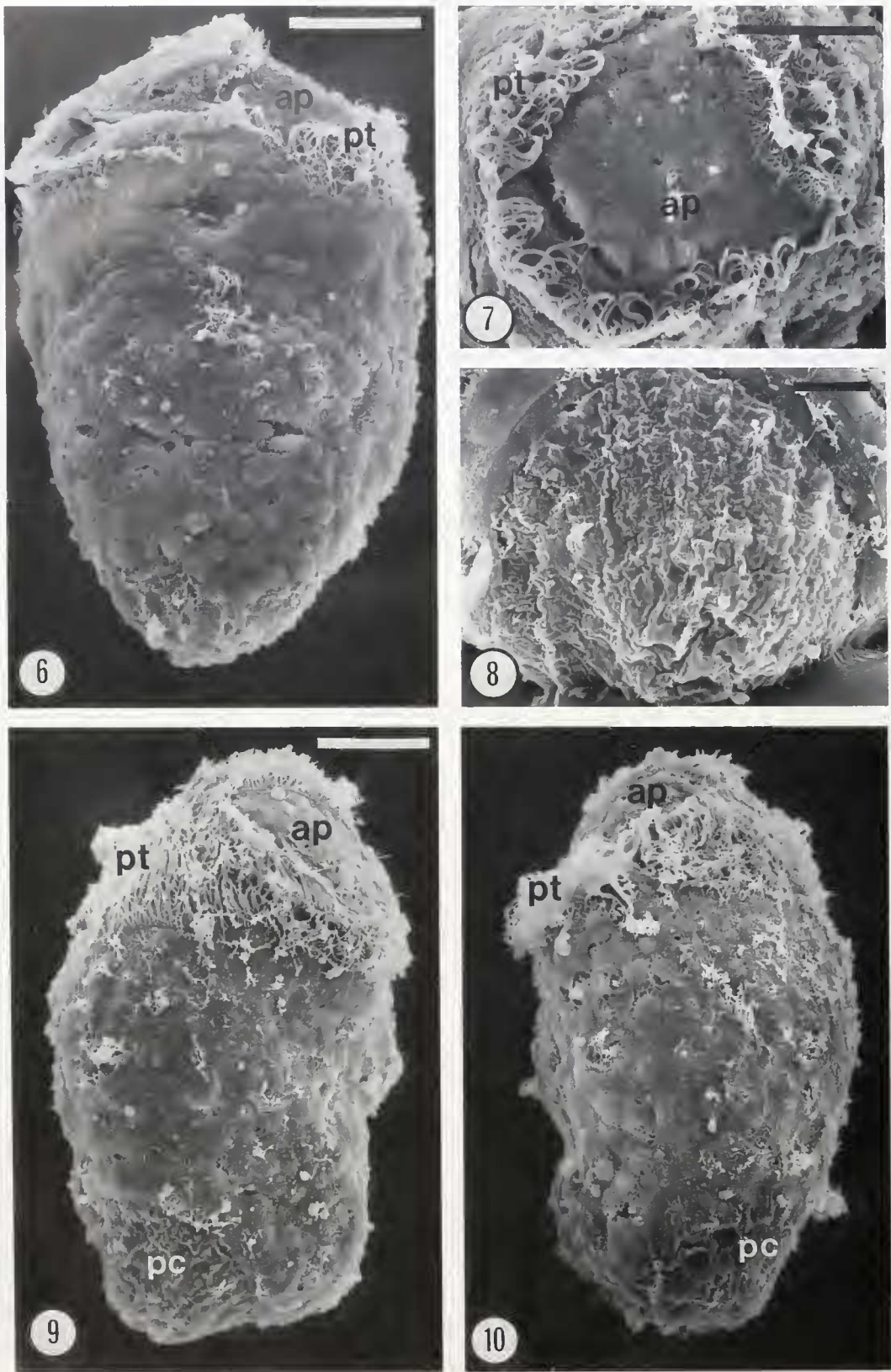
Fifty-six orange egg capsules, each shaped like an inflated oval or pouch and measuring  $3.6 \pm 0.5$  mm in length,  $1.3 \pm 0.3$  mm in width, and  $3.6 \pm 0.7$  mm in height were collected during "Alvin" Dives 1418 and 1419 on the Endeavour Segment of the Juan de Fuca Ridge in 1984 (Tables I, II). Each capsule was attached to the substrate by a flattened basal membrane (Figs. 22, 23). A lateral ridge rose abruptly from the thin basal membrane at either end of the capsule. About 2 mm above the substratum, the ridges at either end of the capsule split into

two wing-like extensions forming a saddle-shaped structure around the central oval escape aperture (Fig. 23B). In most cases an amorphous, poorly fixed, orange embryonic mass, containing an indeterminate number of embryos, occupied the capsule chamber (Figs. 22, 23C). In other cases, from one to six, but most often five, larvae were observed through the capsule walls. The Juan de Fuca Ridge egg capsule wall consisted of two compact dense layers: an outer and an inner layer separated by a sharp boundary (Fig. 24).

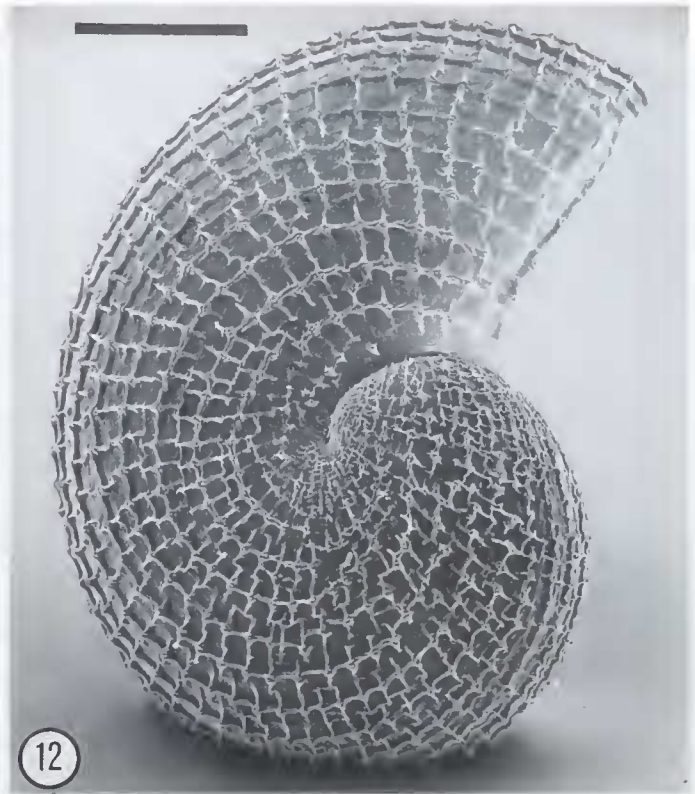
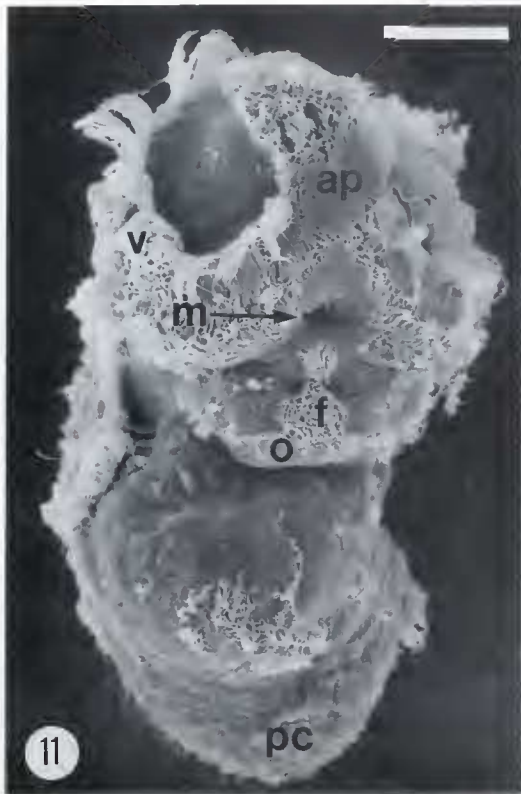
Examination of the amorphous yolk mass present in most capsules revealed that some larval shell had been secreted, but structural details were indeterminable. Nurse eggs may have been present, but fixation was too poor for this to be determined. However, more advanced larvae were present in a few capsules, which revealed a paucispiral protoconch that was large and bulbous and lacked ornamentation other than that due to weak growth lines (Figs. 25, 26).

#### Discussion

Although some archeogastropods embed their eggs in a benthic gelatinous mass or ribbon, the majority of shallow-water archeogastropods do not produce benthic egg capsules (Fretter and Graham, 1962; Hyman, 1967; Robertson, 1976; Webber, 1977; Bandel, 1982; Fretter, 1984; Soliman, 1987; M. F. Strathmann, 1987). Therefore, egg capsules described in this paper from hydrothermal vents are most likely the spawn of prosobranchs of the higher orders Mesogastropoda or Neogastropoda. Various authors (Anderson, 1960; Amio, 1963; Bandel, 1976a, b; Soliman, 1987) have stressed that the general form of the

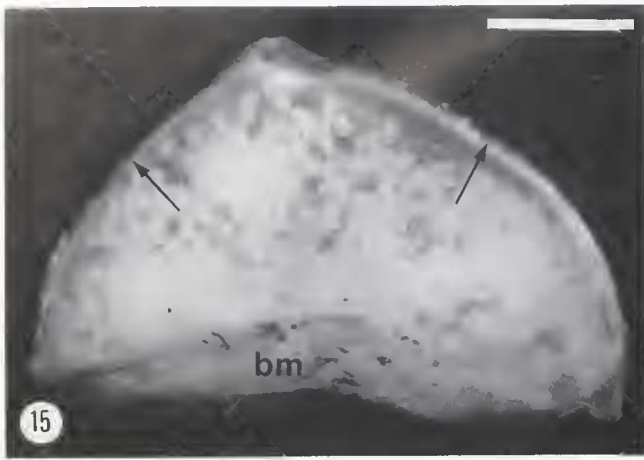


**Figures 6–10.** Scanning electron micrographs of early trochophore larvae removed from Galapagos Rift lenticular egg capsules. **Figure 6.** Ventral view showing apical plate (ap), prototroch (pt), and mouth (m). Scale bar = 25  $\mu\text{m}$ . **Figure 7.** Apical view showing apical plate (ap) and prototroch (pt). Scale bar = 20  $\mu\text{m}$ . **Figure 8.** Early protoconch at extreme posterior end. Scale bar = 10  $\mu\text{m}$ . **Figure 9.** Right lateral aspect showing apical plate (ap), prototroch (pt), and protoconch (pc). Scale bar = 25  $\mu\text{m}$ . **Figure 10.** Left lateral aspect of different specimen to that shown in Figure 9. Scale as in Figure 9. ap, apical plate; pt, prototroch; pc, protoconch.



**Figures 11–14.** Scanning electron micrographs of early and late veliger larvae extracted from lenticular egg capsules from the Galapagos Rift. **Figure 11.** Early veliger larva showing apical plate (ap), velum (v), mouth (m), foot primordium (f), operculum (o), and protoconch (pc). Scale bar = 25  $\mu$ m. **Figure 12.** Apical view of Protoconch I in larva near hatching. Scale bar = 50  $\mu$ m. **Figure 13.** Apertural view of Protoconch I in larva near hatching. Scale bar = 25  $\mu$ m. o, operculum. **Figure 14.** Ventral view of Protoconch I in larva near hatching. Scale bar = 50  $\mu$ m.





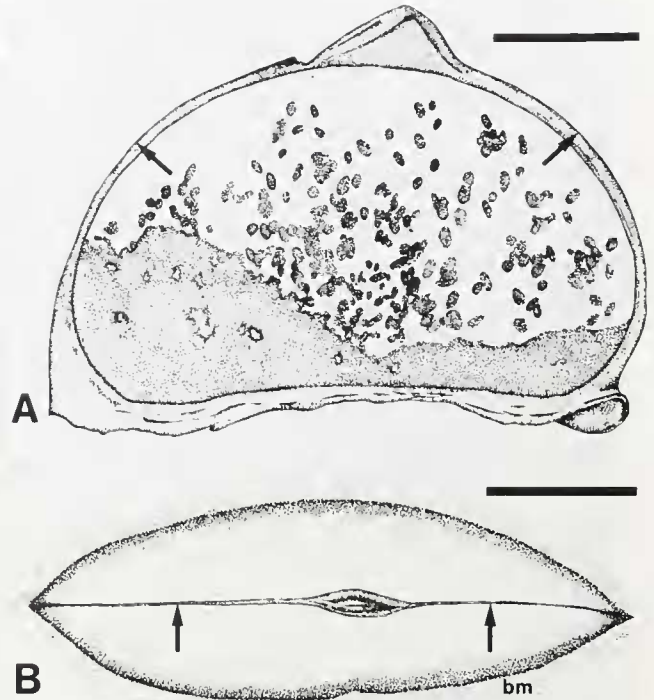
**Figure 15.** Light micrograph of convex side of Galapagos Rift inflated triangular egg capsule with embryos visible through the transparent capsule wall. Arrows mark the lateral ridges. Scale bar = 1 mm. bm, basal membrane.

oothecae in different gastropod taxa is characteristic of the species, and in some cases, of higher orders of classification, and may be valuable in taxonomy. It should be noted, however, that similar capsules may be produced by taxonomically diverse species, while in other cases interspecific variation in capsule morphology is insufficient to differentiate closely related species (Kohn, 1961).

#### *Galapagos Rift lenticular egg capsules*

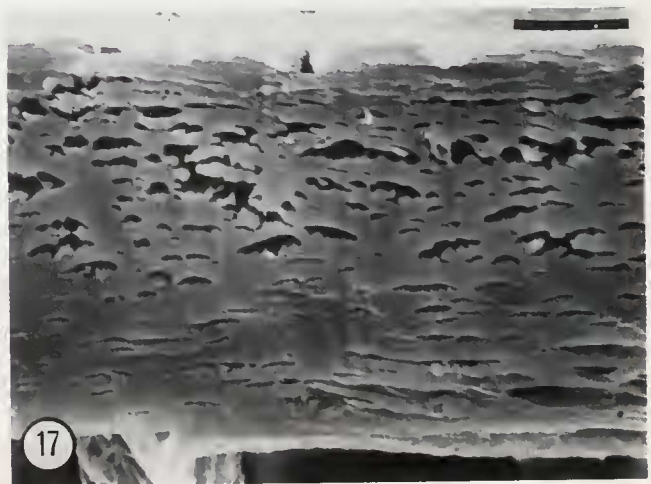
Flattened lenticular egg capsules with a centrally located escape aperture are known from the neogastropod families Muricidae, Fasciolaridae, and Turridae. Dimensions and other statistics pertaining to selected lenticular egg capsules from these families are presented in Table III. The only member of these families known to occur at the Galapagos Rift hydrothermal vents is a large turrid, provisionally described as *Phymorhynchus* sp. (Warén and Bouchet, 1989). A similar species occurs at 13°N and 21°N on the East Pacific Rise (Turner *et al.*, 1985; Warén and Bouchet, 1989). Both the six egg capsules described by Turner *et al.* (1985) and the five "lens-shaped" egg cases described by Berg (1985) as characteristic of turrids, as well as, the lenticular egg capsules described in this paper, may all belong to *Phymorhynchus* sp. from the Galapagos Rift. Differences in reported average size between these three groups of capsules is not unexpected, because capsule size in neogastropods is proportional to adult size. Capsule size is also correlated with female foot width: the capsule is formed and manipulated by the foot during deposition (Robertson, 1976; Shimek, 1986).

Berg (1985) estimated that "lens-shaped" oothecae from the Garden of Eden and Mussel Bed hydrothermal vent sites along the Galapagos Rift contained from 500–1000

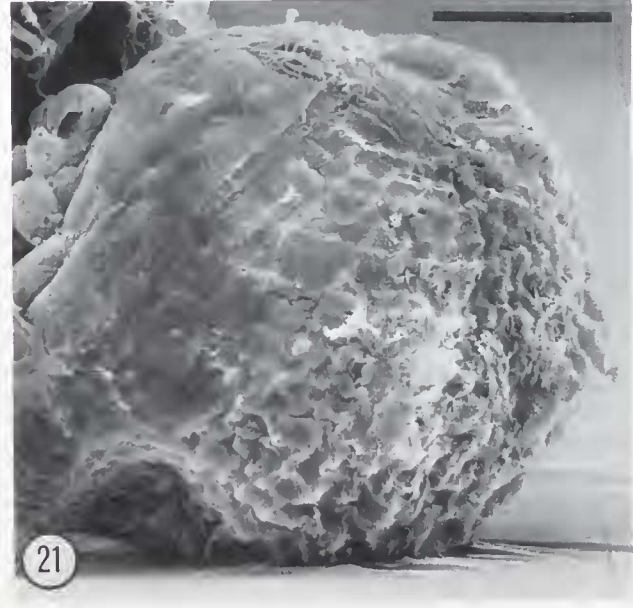
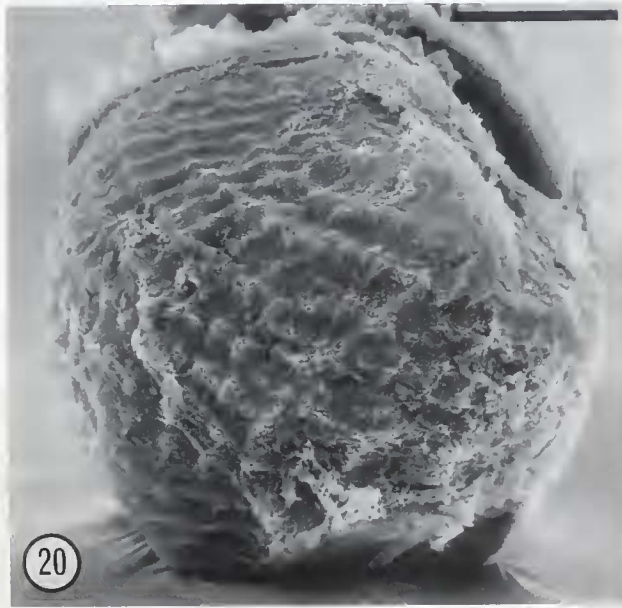
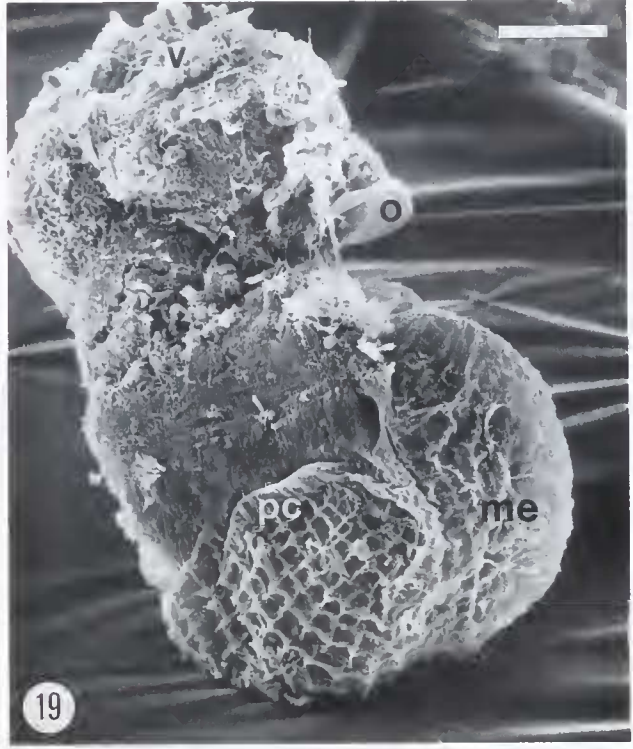


**Figure 16.** (A) View of the convex side of Galapagos Rift inflated triangular egg capsule with individual embryos visible through transparent membrane. Arrows mark the lateral ridges. Scale bar = 1 mm. (B) Apical view of Galapagos Rift inflated triangular egg capsule. Arrows mark the lateral ridges. Scale bar = 1 mm. bm, basal membrane.

eggs with a mean size of  $192.1 \pm 13.5 \mu\text{m}$  by  $136.2 \pm 10.1 \mu\text{m}$ . This agrees well with our count of 1052 larvae in one capsule from Dive 2031 and with the size of larvae both from this capsule (234  $\mu\text{m}$  maximum diameter) and from



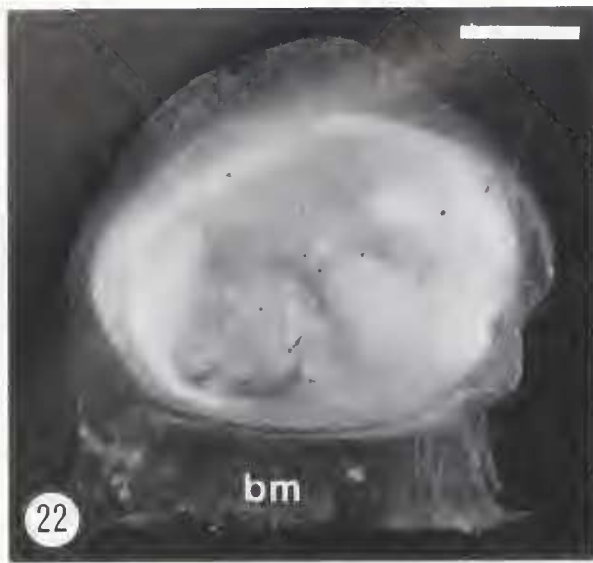
**Figure 17.** Scanning electron micrograph of cross-section of single-layered spongy capsule wall of inflated triangular egg capsule from Galapagos Rift. The outer surface is towards the top. Scale bar = 5  $\mu\text{m}$ .



**Figures 18–21.** Scanning electron micrographs of veliger larvae extracted from inflated triangular egg capsules from Galapagos Rift. **Figure 18.** Lateral ventral view showing velum (v), apical plate (ap), mouth (m), foot primordium (f), and early protoconch (pc). Scale bar = 25  $\mu\text{m}$ . **Figure 19.** Lateral view showing cancellate or net-like early protoconch (pc) sculpture and obscuring membrane (me). Scale bar = 25  $\mu\text{m}$ . o, operculum; v, velum. **Figure 20.** Apical view of early protoconch. Scale bar = 20  $\mu\text{m}$ . **Figure 21.** Dorsal view of early protoconch. Scale bar = 20  $\mu\text{m}$ .

capsules with larvae in earlier stages of development (175  $\mu\text{m}$  in length by 100  $\mu\text{m}$  in width). The absence of nurse eggs further suggests these capsules were laid by a turrid, because nurse eggs are unknown in the Turridae (Table III).

Although the basal diameter of lenticular egg capsules described herein (14.8  $\times$  14 mm) is larger than the 2–6 mm of normal turrid egg capsules, it is not unprecedented. Egg capsules of the turrid *Mangelia plicosa* are 30–33



**Figure 22.** View of the convex side of Juan de Fuca Ridge pouch-like egg capsule containing amorphous embryonic mass. Scale bar = 1 mm. bm, basal membrane.

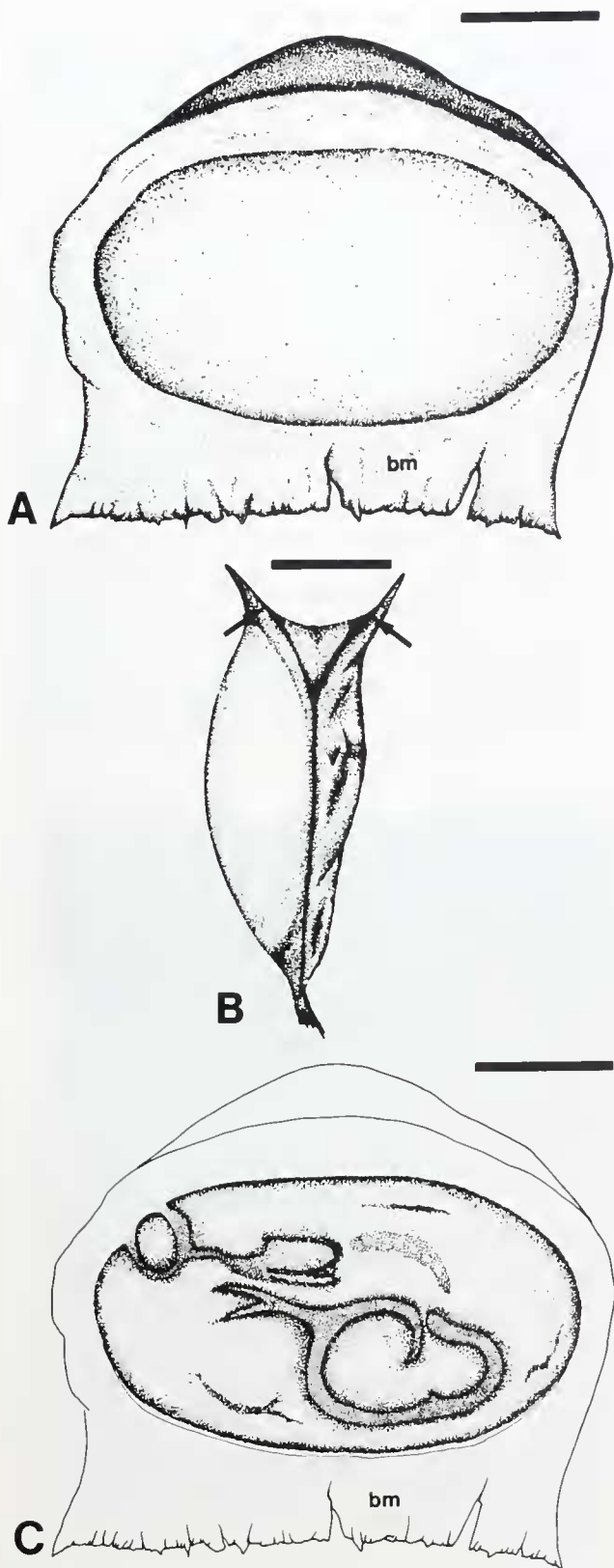
mm in diameter, while those of *Polystira barretti* measure up to 10.7 mm in basal diameter (Table III). Furthermore, the large size of the Galapagos Rift turrid (up to 74 mm in height, pers. obs., RGG) is consistent with the large size of the egg capsules. Although turrid egg capsule wall structure has not been previously studied, the three-layered capsule wall (Fig. 4) is similar to that described for the closely related Conidae (D'Asaro, 1988). This is consistent with the designation of these capsules as belonging to a turrid, because lenticular capsules of the Muricoidea have four layers (D'Asaro, 1988). Some degree of reproductive synchrony may occur in the population of the Galapagos Rift turrid provisionally described as *Phymorhynchus* sp., because eggs, embryos, and larvae contained in different lenticular capsules collected during March 1985 and May 1988 in the present study (Tables I, II), and by Berg (1985), were at the same relative stage of development on each collection date but were at different stages of development between collection dates.

#### *Galapagos Rift inflated triangular capsules*

Berg's (1985) account of four egg capsules, each "shaped like a small inflated triangle," retrieved from a larval trap in 1979 at the Garden of Eden vent on the Galapagos Rift, agrees in every respect with the description found here of the inflated triangular capsules from Rose Garden vent. Although Berg (1985) does not give a measure of the egg capsule's height, the average length of 4.9 mm and width of 1.7 mm of his capsules is similar to the average length of 4.1 mm and width of 1.3 mm for the three inflated triangular capsules described in this report.

Inflated triangular capsules from the Galapagos Rift vent fields are similar in morphology, but not in size, to those from 5480 m in the Kermadec Trench illustrated by Bouchet and Warén (1985a) and attributed to the buccinid *Calliloconcha knudseni* Bouchet and Warén. These 15 mm long by 12 mm high *C. knudseni* capsules were empty and had been drilled by a predator. Certain small capsules similar to the inflated triangular capsules found at the Galapagos Rift, but without a prominent lateral and apical ridge, are produced by members of the neogastropod family Columbellidae (Petit and Risbec, 1929; Thorson, 1940a; Bacci, 1947; Amio, 1955; Bandel, 1974a). Capsules of this group contain no more than 60 eggs, which are usually reduced in number through oophagy (Bandel, 1974a). Small capsules attributed to the buccinid *Tacita danielsseni* (Friele) and to the turrid *Oenopota ovalis* (Friele) from abyssal parts of the Norwegian Sea resemble the inflated triangular capsules in size but appear to lack the lateral ridge and strong off-center apex (Bouchet and Warén, 1979a). The egg capsule attributed to *O. ovalis* in Bouchet and Warén (1979a, Fig. 15) is unlike any known for the genus *Oenopota* (Thorson, 1935; Shimek, 1983b, 1986) or for any other turrid. Capsules belonging to *T. danielsseni* contained thousands of small eggs, although only one large embryo (4 mm in maximum dimension) developed in each capsule. A large protoconch (840–880  $\mu\text{m}$ ) is also present in *O. ovalis*, which is indicative of direct development (Bouchet and Warén, 1979a; Rex and Warén, 1982). By comparison to the above species, several hundred veligers were present in each of the triangular capsules from the Galapagos Rift examined in this study. Neither a buccinid nor a columbellid has as yet been reported from the Galapagos Rift hydrothermal vents.

Gastropods that are large enough to have laid these capsules at the Galapagos Rift vent sites include *Phymorhynchus* sp., *Provanna ios* Warén and Bouchet and *P. muricata* Warén and Bouchet (Warén and Bouchet, 1986, 1989). The turrid *Phymorhynchus* is an unlikely candidate because the capsule type for this species has been provisionally assigned in the present study. Although the inflated triangular capsules from the Galapagos Rift are unlike the typical lenticular capsules of turrids, a similar capsule from the deep-sea has been attributed to the turrid *Oenopota ovalis* (Bouchet and Warén, 1979a; see discussion above). Either species of *Provanna* is also an unlikely choice, because the recent placement of *Provanna* within the Littorinoidea (Warén and Bouchet, 1989) suggests that the production of such an elaborate egg capsule is unlikely, because all known littorinoids spawn either a benthic, amorphous gelatinous mass, a single pelagic capsule containing a single egg, or release veligers or fully formed juveniles from an internal brood pouch (Thorson, 1946; Anderson, 1960, 1962; Amio, 1963; Pilkington,



**Figure 23.** (A) View of the convex side of Juan de Fuca Ridge egg capsule. Scale bar = 1 mm. bm, basal membrane. (B) Lateral view of Juan de Fuca capsule showing lateral ridge running into two apical wing-

1974; Robertson, 1976; Bandel, 1974b, 1975b, 1982; Soliman, 1987; M. F. Strathmann, 1987). Based on egg capsule morphology, we cannot assign the inflated triangular egg capsules from the Galapagos Rift to a particular species. A more definitive statement on the taxonomic affiliation of the inflated triangular capsule must await additional collections of organisms from the Galapagos Rift vent fields and further taxonomic examination of existing material.

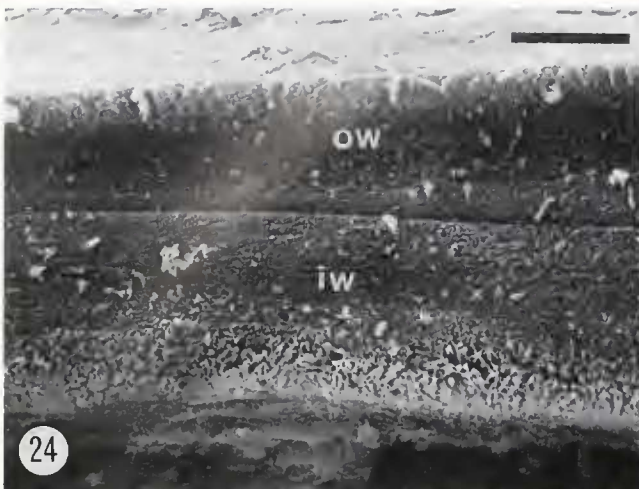
The wall structure of the inflated triangular egg capsules from the Galapagos Rift is similar to that seen in several species within the Muricoidea (Roller and Stickle, 1988; D'Asaro, 1988), although too little is known of egg capsule wall structures at this time to make a definitive statement as to this capsule's affinity. Because all three inflated triangular capsules collected from Galapagos Rift on three separate dives in 1985 contained early veligers at the same stage of development, it is possible that some degree of reproductive synchrony occurs in this population.

#### *Juan de Fuca Ridge egg capsules*

Egg capsules strikingly similar in size and shape to the Juan de Fuca Ridge capsules described in the present study are produced by the cancellariid neogastropod, *Admete viridula* (Fabricius) [Thorson, 1935: fig. 71 (mistakenly attributed to *Volutina undata* Brown, see Thorson, 1944: 108); Bouchet and Warén, 1985b: fig. 687]. The capsules described herein and those of *A. viridula* both possess parallel wing-like extensions, a flattened base, and an apical escape aperture. Species of *Admete* have been described from 6700 m deep in the Kermadec Trench, whereas *A. viridula*, which is circumpolar, has a depth range of 4–2,295 m, according to Clarke (1962). The small number (1–6) of large larvae present in Juan de Fuca capsules is consistent with the 6–7 larvae per capsule found in *Admete viridula* by Thorson (1935) and the 6 larvae per capsule found in *Admete* sp. by MacGinitie (1955). However, a species of *Admete* has not been collected from the Juan de Fuca Ridge.

Other pouch-like egg capsules, with or without a flattened base, but without wing-like extensions, are found in the neogastropod families Muricidae and Buccinidae (Thorson, 1935, 1940b; Anderson, 1960; Golikov, 1961; Cowan, 1964; Radwin and Chamberlin, 1973; MacIntosh, 1979, 1986; D'Asaro, 1986). However, buccinids typically form their capsules into clusters (Thorson, 1935; Cowan, 1964), in contrast to the pouch-like capsules from Juan

like extensions (arrows) forming a saddle-like structure. Scale bar = 1 mm. (C) View of the convex side of Juan de Fuca egg capsule with amorphous embryonic mass visible through transparent capsule wall. Scale bar = 1 mm. bm, basal membrane.



**Figure 24.** Scanning electron micrograph of cross-section of double-layered capsule wall of Juan de Fuca Ridge egg capsule. Scale bar = 5  $\mu\text{m}$ . ow, outer wall; iw, inner wall.

de Fuca, which are individually attached to the substrate. Capsules secreted by members of the neogastropod family Columbelloidea frequently possess apical collars that sur-

round a central escape aperture somewhat similar to the wing-like extensions seen in capsules from the Juan de Fuca Ridge described in the present study (Thorson, 1940a; Perry and Schwengel, 1955; Amio, 1955, 1963; Marcus and Marcus, 1962; Scheltema, 1969; D'Asaro, 1970b; Bandel, 1974a).

Only two gastropods, *Buccinum viridum* Dall and *Provananna variabilis* Warén and Bouchet, which are large enough to have secreted these capsules, have been recorded from the Juan de Fuca Ridge system (Warén and Bouchet, 1986; Tunnicliffe *et al.*, 1985; Tunnicliffe and Fontaine, 1987; Tunnicliffe, 1988). Dall (1890) described *B. viridum* as having a maximum shell height of 46 mm, while *P. variabilis* reaches a maximum height of 8.7 mm (Warén and Bouchet, 1986). Warén and Bouchet (1989) have recently placed *P. variabilis* within the Superfamily Littorinoidea. No members of the Littorinoidea have as yet been shown to produce complex egg capsules (see discussion above of inflated triangular capsules), which suggests that *P. variabilis* is not the source of the egg capsule from the Juan de Fuca Ridge. The Buccinidae produce egg capsules either singly or in clusters, each containing many nurse eggs; only a few of these survive (Thorson, 1935, 1946; Lebour, 1937; Anderson, 1960). Encapsulated



**Figures 25–26.** Scanning electron micrographs of larvae extracted from Juan de Fuca Ridge egg capsules. **Figure 25.** Lateral view of protoconch showing height of the first whorl and weak concentric growth lines. Scale bar = 200  $\mu\text{m}$ . **Figure 26.** Apical view showing unsculptured appearance of protoconch. Scale bar = 200  $\mu\text{m}$ .

Table III

Taxonomic affiliation, dimensions, number of eggs, egg size, and number of veligers present at hatching for lenticular egg cases as reported in selected references

Species	Size (mm)		Number of eggs	Egg size ( $\mu\text{m}$ )	Number of veligers at hatching	Post-hatching development type	Reference
	Basal diameter	Height					
Order Neogastropoda							
<b>Muricoidea</b>							
<b>Family Muricidae</b>							
<i>Bedevela hanleyi</i> (Angas)	3.0	—	50–70	250	15	N	Anderson, 1965
<i>Bedevelina (Lataxiena) birileffi</i> (Lischke)	3.0	0.85	60–90	190	—	P	Amio, 1963
<i>Ergalatax constrictus</i> (Reeve)	2.5–3.0	—	130	—	—	?	Habe, 1960
<i>Ergalatax calcareus</i> (Dunker)	3.5–4.5	—	130	—	—	?	Habe, 1960
<i>Trophon clathratus</i> (L.)	6–7	—	—	—	9–18	N	Thorson, 1940b
<i>Trophon muricatus</i> (Montagu)	2.5	—	—	—	2–9	N	Lebour, 1936
<i>Trophon truncatus</i> (Strom.)	1.8–3.1	—	—	—	6–11	N	Thorson, 1946
<i>Zeatrophon (Xymene) ambiguus</i> (Philippi)	6–10	1.0–1.5	—	—	600	N-P	Pilkington, 1974
<b>Family Fasciolaridae</b>							
<i>Glaphyrina vulpicolor</i> (Sowerby)	12	—	—	—	10	N	Pilkington, 1974
<b>Conoidea</b>							
<b>Family Turridae</b>							
<i>Clavus japonicus</i> (Lischke)	2.5	1.8	2–4	650	2–4	N	Amio, 1963
<i>Crassispira</i> sp.	1.5	—	2–5	—	2–5	N	Bandel, 1976b
<i>Drillia crenularis</i> (Lamarck)	6–7	—	150–170	230–300	150–170	P	Thorson, 1940a
<i>Drillia solida</i> (C. B. Adams)	4	1	2–7	—	2–7	?	Bandel, 1976b
<i>Kurtziella plumbea</i> (Hinds)	2.3 $\pm$ 0.3	—	180 $\pm$ 43	137 $\pm$ 8	180 $\pm$ 43	?	Shimek, 1983c
<i>Mangelia nebula</i> (Montagu)	1.6	—	—	—	60	P	Lebour, 1934, 1936, 1937
<i>Mangelia plicosa</i> (C. B. Adams)	30.1–33.0	0.32	60	160	—	?	Perry and Schwengel, 1955
<i>Oenopota simplex</i> (Midd.)	2–3	—	—	—	5–6	N	Thorson, 1935
<i>Oenopota exarata</i> (Moller)	3.0–4.5	—	—	—	5–21	N	Thorson, 1935
<i>Oenopota bicarinata</i> (Couth.)	2.25–3.25	—	—	—	3–11	N	Thorson, 1935
<i>Oenopota pyramidalis</i> (Strom.)	3.5–6	—	—	—	4–20	N	Thorson, 1935
<i>Oenopota nobilis</i> (Moller)	4.5–4.75	—	—	—	3–7	N	Thorson, 1935
<i>Oenopota trevelyana</i> (Turton)	3.1–3.3	—	—	—	25–31	N-P	Thorson, 1946
<i>Oenopota turricola</i> (Montagu)	2.5	—	100–150	—	100–150	?	Vestergaard, 1935
<i>Oenopota elegans</i> (Moller)	3.02	—	250	150	250	P	Shimek, 1983b
<i>Oenopota excurvata</i> (Carpenter)	2.08	1.08	30	212	—	?	Shimek, 1983b
<i>Oenopota fiducula</i> (Gould)	2.24	0.98	20	371	—	?	Shimek, 1983b
<i>Oenopota levidensis</i> (Carpenter)	5.30	1.38	175 $\pm$ 85	286	175 $\pm$ 85	P	Shimek, 1983b
<i>Ophiodermella inermis</i> (Hinds)	4.68 $\pm$ 0.99	1.44 $\pm$ 0.29	208 $\pm$ 61	222 $\pm$ 15	208 $\pm$ 61	P	Shimek, 1983a
<i>Philbertia gracilis</i> (Montagu)	3.4	—	—	—	40–80	P	Lebour, 1934, 1936, 1937
<i>Philbertia linearis</i> (Montagu)	1.5–2.0	—	60–80	140–150	—	P	Lebour, 1934, 1936, 1937
	—	—	51–114	150	—	P	Thorson, 1946
<i>Philbertia purpurea</i> (Montagu)	5.3	0.6	350–400	100	—	P	Franc, 1950
<i>Polystira barretti</i> (Guppy)	5.0–10.7	—	32–126	438	32–126	N	Penchaszadeh, 1982
<i>Raphitoma (Teretia) amoena</i> (Sars)	1.25–1.5	—	—	—	2	N	Thorson, 1935
Unknown turrid	2–3.5	—	—	—	—	?	Arnaud and Zibrowius, 1973
Unknown turrid	2.6	—	—	—	—	?	Bouchet and Warén, 1980
Unknown turrid	4.0–4.2	—	—	—	—	?	Bouchet and Warén, 1980

direct development is universal within this group (Lebour, 1937; Robertson, 1976; Colman *et al.*, 1986; Warén and Bouchet, 1989), although planktotrophic buccinids are known from the Early Tertiary (Hansen, 1982). Capsule

wall morphology of the Juan de Fuca egg capsule described in the present study is similar to that seen in certain Buccinidae and Muricidae (D'Asaro, 1988), although a definitive statement is not possible until the micromorphology

of a wider taxonomic grouping of capsules is known. On the basis of egg capsule morphology we are unable to assign the pouch-like egg capsules from the Juan de Fuca Ridge to any species that has as yet been collected from this site. However, the similarity of the Juan de Fuca Ridge capsules to those produced by species of *Admete* (Thorson, 1935; Bouchet and Warén, 1985b) is so striking that it leads us to predict that a member of this genus may soon be found associated with this hydrothermal vent.

#### *Egg size, fecundity, and protoconch morphology*

The size of the ovum in those prosobranch gastropods that do not provide nurse eggs or albumen in the egg capsule regulates the amount of nutrition supplied to the larva and has a close relationship with the type of larval development [Thorson 1946, 1950; Shuto, 1974; Bandel, 1975a; Lima and Lutz, 1990; but see discussion on this topic in Vance (1973, 1974), Underwood (1974), Steele (1977), Strathmann (1977), Perron (1981), Todd and Doyle (1981), and Hines, (1986)]. Planktotrophic prosobranch gastropod larvae typically have a small pointed apex, often with delicate sculpture, reflecting an originally small ovum. However, non-planktotrophic larvae typically have a large rounded apex reflecting a large ovum with plenty of yolk available for the larva to grow to a large size (Ockelmann, 1965; Shuto, 1974). This relationship may become obscured in those non-planktotrophs that feed on nurse eggs or other forms of extraembryonic nutrition and emerge as large juveniles, because they often have egg diameters no larger than those of free-swimming, non-planktotrophs (Bandel, 1975a, c; Jablonski, 1986). Similarly, Hadfield and Strathmann (1990) have shown that egg size is not a reliable indicator for differentiating between a pelagic and a benthic mode of development in non-planktotrophic trochoidean archeogastropods. In addition, although archeogastropods are purported to be exclusively non-planktotrophic (Anderson, 1960; Helsinga, 1981; Strathmann, 1978a, b; Rex and Warén, 1982; Lutz *et al.*, 1984; Jablonski, 1985; Warén and Bouchet, 1989), many species develop from relatively small eggs between 110 and 230  $\mu\text{m}$  in diameter (Amio, 1963), and as small as 80  $\mu\text{m}$  in some cases (Bandel, 1982). Unfortunately, egg size criteria could not be applied in the present study, because ova were not encountered.

In the absence of nurse eggs, the number of eggs produced by a gastropod species is also indicative of its mode of larval development (Thorson, 1950; Crisp, 1978; Shuto, 1974; Bandel, 1975a). A large number of eggs suggests planktotrophic development, because many free-swimming embryos and larvae are assumed to be lost to predation, whereas few eggs suggest non-planktotrophic development (Thorson, 1950; Jablonski and Lutz, 1983). Estimates of fecundity in the present study are compli-

cated by the fact that we have no way of knowing how many capsules were produced by each laying female. However, the over 1000 larvae contained in the lenticular capsules from the Galapagos Rift, when compared to information on the number of eggs per capsule, total fecundity, and development type in other species with lenticular egg capsules (Table III), suggests that this species develops planktotrophically following hatching. The apparent absence of nurse eggs and the presence of several hundred embryos in the inflated triangular capsules from the Galapagos Rift also suggests the potential for planktotrophic development after hatching; while the small number of embryos (1–6) in pouch-like capsules from the Juan de Fuca Ridge is strongly indicative of non-planktotrophic development.

Non-planktotrophic development is the most common strategy among prosobranchs in the deep-sea, soft-sediment environment of the western North Atlantic (Rex and Warén, 1982). However, an examination of bathyal and abyssal prosobranch larval shells reveals that roughly 30% may develop planktotrophically below 1000 m in the north-eastern Atlantic (Bouchet, 1976a, b; Bouchet and Warén, 1979b) and that the incidence of planktotrophic development in this group increases with depth below the continental shelf (Rex and Warén, 1982). About 50% of mesogastropod and neogastropod prosobranch species on the abyssal plain may have planktotrophic development based on their protoconch morphologies (Rex and Warén, 1982). Bouchet (1976a, b) and Bouchet and Warén (1979b) have proposed that deep-sea prosobranch larvae with protoconchs, indicative of planktotrophy, migrate to feed and undergo development in surface waters. In addition,  $^{18}\text{O}$  and  $^{13}\text{C}$  isotope analyses of larval shells from deep-sea gastropods have suggested that at least some larvae of abyssal species may migrate upwards into warmer waters during development (Bouchet and Fontes, 1981; Killingley and Rex, 1985).

Protoconch I sculpture of the type seen in larvae from lenticular egg capsules at the Galapagos Rift (Figs. 12–14) is characteristic of many turrid species with putative planktotrophic development in both shallow waters [*Philbertia linearis* (Montagu) (Rodriguez Babio and Thiriot-Quiévreux, 1974), *Raphitoma* spp. (Richter and Thorson, 1975)] and in the deep sea [*Pleurotomella* spp., *Teretia* spp., *Xanthodaphne* spp., *Phymorhynchus* spp., *Gymnobela* spp., *Theta* spp. (Bouchet and Warén, 1980), *Gymnobela subaraneosa* (Dautzenberg and Fischer) (Colman *et al.*, 1986)]. The Turridae includes species with larval shell morphologies that are indicative of both planktotrophic and non-planktotrophic development (Rex and Warén, 1982; Shimek, 1983a, b, c, 1986). The maximum diameter of the Protoconch I in certain planktotrophic-type turrid species can be roughly estimated from published micrographs, including the species *Phil-*

*bertia linearis* (260  $\mu\text{m}$ ) (Rodríguez Babio and Thiriou-Quévieux, 1974), *Raphitoma reticulata* (Renier) (220  $\mu\text{m}$ ), *R. (Philbertia) purpurea* (Montagu) (245  $\mu\text{m}$ ), *R. (Cirilla) linearis* (Montagu) (245  $\mu\text{m}$ ), *R. (Leufroyi) leufroyi* (Michaud) (225  $\mu\text{m}$ ) (Richter and Thorson, 1975), *Pleurotomella coeloraphe* (Dautzenberg and Fischer) (265  $\mu\text{m}$ ), *Pleurotomella demosia* (Dautzenberg and Fischer) (355  $\mu\text{m}$ ), *Pleurotomella megalembryon* (Dautzenberg and Fischer) (280  $\mu\text{m}$ ), *Pleurotomella bureaui* (Dautzenberg and Fischer) (220  $\mu\text{m}$ ), *Pleurotomella sandersoni* Verrill (195  $\mu\text{m}$ ), *Teretia teres* (Forbes) (260  $\mu\text{m}$ ), *Xanthodaphne dalmasi* (Dautzenberg and Fischer) (215  $\mu\text{m}$ ), *Theta chariessa* (Watson) (240  $\mu\text{m}$ ) (Bouchet and Warén, 1980), and *Gymnobela subaraneosa* (Dautzenberg and Fischer) (180  $\mu\text{m}$ ) (Colman *et al.*, 1986).

Assuming that the larvae in lenticular egg capsules from the Galapagos Rift retrieved on "Alvin" Dive 2031 were near hatching and represent the complete Protoconch I stage, then measurements made from electron micrographs reveal that this species has a Protoconch I maximum diameter of approximately 235  $\mu\text{m}$  (Figs. 12–14). This compares favorably with the Protoconch I maximum diameters above, estimated for various turrid species (195–280  $\mu\text{m}$ ), with the exception of the large Protoconch I in *Pleurotomella demosia* (355  $\mu\text{m}$ ) and the small Protoconch I in *Gymnobela subaraneosa* (180  $\mu\text{m}$ ). The maximum diameter of the Protoconch I in larvae from the lenticular capsules also agrees well with the size of the Protoconch I (as estimated from published micrographs) in both the unnamed, newly settled turrid from the Galapagos Rift (205–225  $\mu\text{m}$ ) and the unnamed newly settled turrid from 21°N on the East Pacific Rise (260  $\mu\text{m}$ ) (Turner *et al.*, 1985; their figs. 27a–e and 26a–e, respectively). Unfortunately, pre-juvenile development is incomplete for larvae in lenticular capsules in the present study, and the final Protoconch II maximum diameter and number of whorls cannot be determined, which precludes the estimation of D/Vol values for these samples. However, as estimated from Fig. 27a in Turner *et al.* (1985), the unnamed newly settled turrid from the Galapagos Rift has a Protoconch II with approximately 4 whorls and a maximum diameter of 950  $\mu\text{m}$  (giving a D/Vol value of 0.19). Similarly, the unnamed newly settled turrid from 21°N (Turner *et al.*, 1985) has a Protoconch II maximum diameter of approximately 775  $\mu\text{m}$  with about 4 whorls (giving a D/Vol value of 0.19), as estimated from Fig. 26d in Turner *et al.* (1985). The number of volutions, D/Vol values, clear demarcation between Protoconch I and II, and the protoconch ornamentation of spiral threads crossed by axial riblets of both unnamed newly settled turrids from the Galapagos Rift and 21°N, depicted in Turner *et al.* (1985), are all indicative of planktotrophic development.

Although the Protoconch I sculpture of the unnamed newly settled turrid from the Galapagos Rift, depicted in Turner *et al.* (1985, their figs. 27a–e), and Protoconch I larvae from lenticular egg capsules in the present study, also from the Galapagos Rift (Figs. 12–14), cannot be directly compared due to corrosion of the former, the similarly sized Protoconchs I (205–225  $\mu\text{m}$  and 235  $\mu\text{m}$ , respectively) suggest that these specimens are taxonomically related. Because the only turrid to be collected at the Galapagos Rift is the provisionally classified *Phymorhynchus* sp. (Warén and Bouchet, 1989), it is likely that both the turrid juvenile from the Galapagos Rift described by Turner *et al.* (1985), and the lenticular egg capsules and larvae within, belong to this species. However, adult or juvenile *Phymorhynchus* sp. with intact, non-corroded protoconchs, characteristics that would verify this identification, have not been collected at the Galapagos Rift.

Although it is not possible to determine the maximum diameter of the Protoconch I stage or the D/Vol value for larvae from the inflated triangular egg capsules from the Galapagos Rift due to the incomplete development of the larval shell, the initial reticulate sculpture (Figs. 19–21) is indicative of planktotrophic development, following the encapsulated phase. This type of sculpture is similar to that seen on the Protoconch I of some members of the mesogastropod families Rissoidae (Lebour, 1936, 1937; Amio, 1963) and Cypraeidae (Richter and Thorson, 1975), as well as the neogastropod families Columbelloidea (Colman *et al.*, 1986) and Turridae (Lebour, 1934; Amio, 1963; Rodríguez Babio and Thiriou-Quévieux, 1974; Richter and Thorson, 1975; Bouchet, 1976a; Bouchet and Warén, 1980). Members of the Cypraeidae have not been collected in the deep-sea (Clarke, 1962), and no member of this family or of the Rissoidae has been collected at the Galapagos Rift. The columbellid *Anachis haliaeeti* (Jeffreys) from the Rockall Trough has an ornately sculptured Protoconch I and has been designated a planktotrophic developer (Colman *et al.*, 1986). Shallow-water species of this genus produce small egg capsules similar to the inflated triangular type from the Galapagos Rift but with a circular collar around the capsule's apex and containing only 10–30 embryos (Scheltema, 1969) in contrast to the several hundred larvae seen in capsules from the Galapagos Rift. Likewise, the morphology of the inflated triangular egg capsule is unlike that seen in most Turridae. However, the egg capsule attributed to the turrid *Oenopota ovalis* (Bouchet and Warén, 1979a) resembles the inflated triangular capsules, but contains only one embryo with an unsculptured protoconch, in contrast to the several hundred highly ornamented larvae encountered in the inflated triangular capsules from the Galapagos Rift. Given the incomplete formation of the larval shell and unique structure of the egg capsule, it has proved impos-



sible to assign the inflated triangular capsules from the Galapagos Rift to any known gastropod species from this site.

Larvae from the Juan de Fuca Ridge egg capsules have a large, paucispiral protoconch devoid of sculpture (Figs. 25, 26), which suggests that this species develops non-planktotrophically. Assuming that these larvae have a nearly fully developed protoconch, with a maximum diameter of approximately 1.3 mm and 1.5 whorls (as estimate from Fig. 26), their calculated D/Vol value of 0.87 in concert with the small number of whorls is also indicative of non-planktotrophic development. This type of protoconch, lacking ornamentation, is similar to that produced by members of the neogastropod superfamilies Muricoidea and Cancellarioidea (Thorson, 1935; Radwin and Chamberlin, 1973; Bandel, 1975a, b, c; Bouchet and Warén, 1985a; Colman *et al.*, 1986; Colman and Tyler, 1988), however taxonomic placement of these larvae is uncertain using protoconch morphology alone. The protoconch of the cancellaroid *Admete viridula* (Thorson, 1935: fig. 72), the species with the most similar egg capsule morphology to the specimens described in this study from the Juan de Fuca Ridge, has a maximum diameter of about 0.88 mm [as estimated from Thorson (1935: fig. 72)] and 1.25 whorls, for a D/Vol value of 0.77, which also compares favorably with that calculated for encapsulated larvae from the Juan de Fuca Ridge (0.87). Bouchet and Warén (1985a) give the protoconch maximum diameters and number of whorls for the deep-sea buccinids *Eosipho thorybopus* Bouchet and Warén (0.7 mm, 1 whorl, D/Vol = 0.7), *Manaria lirata* Kuroda and Habe (0.8 mm, 1+ whorl, D/Vol = 0.8), and *M. clandestina* Bouchet and Warén (0.7 mm, 1+ whorl, D/Vol = 0.7). Colman *et al.* (1986) also provide protoconch maximum diameters, whorl number, and D/Vol values for the deep-sea buccinids *Tacita abyssorum* (Locard) (0.75 mm, 1.2 whorls, D/Vol = 0.63), *Colus jeffreysianus* (Fischer) (2.5 mm, 1.25 whorls, D/Vol = 2), and the muricid *Trophon* sp. (1.1 mm, 1.5 whorls, D/Vol = 0.73). All of these species lack protoconch ornamentation. Ornamentation is also lacking on some members of the mesogastropod families Rissoidae (Richter and Thorson, 1975) and Cerithiidae (Rodríguez Babio and Thiriou-Quévieux, 1974), as well as the neogastropod families Nassariidae (Richter and Thorson, 1975) and Turridae (Bouchet and Warén, 1980; Colman *et al.*, 1986).

Protoconchs retained on adult specimens of the two known gastropod species from the Juan de Fuca Ridge, large enough to have laid the capsules from this site [*Buccinum viridum* (pers. obs.) and *Provanna variabilis* (Warén and Bouchet, 1986)], were badly corroded, precluding comparison with larvae extracted from the Juan de Fuca Ridge egg capsules. The potential for either of these two

species to be the source of the pouch-like capsules from the Juan de Fuca Ridge is discussed above.

#### *Molluscan larval dispersal at hydrothermal vents*

Despite the ephemeral nature and patchy distribution of hydrothermal vent environments, an analysis of the developmental mode of 30 species of mollusks (gastropods and bivalves) present at three deep-sea hydrothermal vents (13°N, 21°N and Galapagos Rift; Lutz *et al.*, 1980, 1984, 1986; Turner and Lutz, 1984; Turner *et al.*, 1985; Lutz, 1988) suggested that only three species (two turrids and a mytilid) have larvae capable of long-range dispersal. The other 27 species have larval shell morphologies indicative of non-planktotrophic, low-dispersal modes of development. These developmental patterns are all typical of the shallow-water members of the systematic group to which these vent species belong. Although some unusual adaptations may be present among larvae of vent organisms, such as prolonged delay of metamorphosis in response to low deep-sea temperatures (Lutz *et al.*, 1980, 1984, 1986; Turner and Lutz, 1984; Turner *et al.*, 1985; Lutz, 1988), inferences made from egg size, fecundity, and larval morphology suggest that unique adaptations to ensure successful larval dispersal between vent habitats have not evolved in hydrothermal vent mollusks (Turner *et al.*, 1985; Warén and Bouchet, 1989). However, many of the molluscan morpho-species described from vents in the eastern Pacific are present at more than one vent field (9 are shared by Galapagos Rift and 13°N; 10 are shared by Galapagos Rift and 21°N; 18 are shared by 13°N and 21°N; 2 are shared by Juan de Fuca and Explorer Ridges; and 7 are shared by Galapagos Rift, 13°N and 21°N) (Boss and Turner, 1980; Kenk and Wilson, 1985; Schein-Fatton, 1985; McLean and Haszprunar, 1987; McLean, 1988, 1989a, b; Warén and Bouchet, 1986, 1989). This paradox may be partially explained by recent findings of vent fauna on or near whale carcasses (Smith *et al.*, 1989; but see Tunnicliffe and Juniper, 1990) and at cold methane and sulfide seeps (Paull *et al.*, 1984; Kennicutt *et al.*, 1985, 1989; Juniper and Sibuet, 1987; Mayer *et al.*, 1988), which may serve as stepping-stone habitats for dispersal between vents. In addition, Johannesson (1988), and to a lesser degree others (Palmer and Strathmann, 1981; Burton, 1983; Highsmith, 1985; Hedgecock, 1986; Jackson, 1986; R. R. Strathmann, 1987; Safriel and Hadfield, 1988; O'Foighil, 1989), question the effective dispersal benefits of the planktotrophic *versus* the non-planktotrophic mode of development, over long distances. It is suggested that a small founder group of direct developers or hermaphroditic individuals, passively transported to a new site as adults or in a drifted egg mass, would have an advantage over planktonic developers in establishing a new colony, because their offspring would remain in the

immediate vicinity of the founder group where the encounter rate with mates would be high. On the other hand, the offspring of planktonic developers are free-swimming for weeks and may settle far from the founder group, and from each other, where the encounter rate with mates is low (Johannesson, 1988).

Similar, if not identical, species of *Phymorhynchus* occur at the Galapagos Rift and at 13°N and 21°N on the East Pacific Rise (Warén and Bouchet, 1989). The planktotrophic-type larvae found in turrinid egg capsules from the Galapagos Rift, putatively identified as the spawn of *Phymorhynchus* sp., suggests that this species has a great potential for dispersal and may explain its apparent wide distribution (but see discussion above). Shimek (1983a, b, 1986) has cultured three shallow-water turrinids, *Ophiodermella inermis* (Hinds), *Oenopota levidensis* (Carpenter), and *Oenopota elegans* (Möller), with encapsulated periods of 50 days, 50 days, and 42–49 days, respectively, and free-swimming periods of 35 days, 7–10 days, and 42–49 days, respectively. In addition, *Oenopota levidensis* assumes a benthic existence and develops for a further 25 days prior to metamorphosis as a “demersal-planktotrophic larva,” using the terminology of Shimek (1986). If parallel conditions obtain in deep-sea turrinids the potential for dispersal of larvae during a 1–7 week planktonic phase, given known bottom currents on the East Pacific Rise (Lonsdale, 1977), would be on the order of hundreds of kilometers (Lutz *et al.*, 1980). A maximum current speed of 18 cm s<sup>-1</sup> was recorded at a site 50 m above the crest of the East Pacific Rise within 350 m of a suspected hydrothermal plume (Lonsdale, 1977). In addition, a decrease in developmental rate in response to cold ambient bottom waters away from the vents may increase the length of larval life and further enhance dispersal (Lutz *et al.*, 1980, 1984, 1986; Turner and Lutz, 1984; Turner *et al.*, 1985; Lutz, 1988). Based on comparison of the stable isotope compositions (<sup>18</sup>O:<sup>16</sup>O ratios) of adult and larval shells, Killingley and Rex (1985) reported that three deep-sea turrinids with similar protoconch sculpture to that seen in *Phymorhynchus* (*Theta lyromiclea*, *T. chariessa* and *Pleurotomella sandersoni*), migrate vertically, as larvae, to develop in warm surface waters. At present, it is indeterminable whether *Phymorhynchus* larvae complete their development as demersal feeders, ascend to feed on plankton in surface waters, or undergo some combination of these developmental modes. The fact that *Phymorhynchus* is either a predator or scavenger at the vents (Warén and Bouchet, 1989) indicates that it may not be restricted to vent habitats, although it is able to tolerate the extreme vent environment and exploit the abundant food energy available at these sites. Adult *Phymorhynchus* are mobile and the extent to which movements of adults aid in dispersal is unknown.

Although it has not been possible to unambiguously identify the species to which the inflated triangular egg capsules from the Galapagos Rift or the pouch-like egg capsules from the Juan de Fuca Ridge belong, we can infer something about the mode of development of these two organisms. The presence of several hundred veliger larvae in inflated triangular capsules from the Galapagos Rift and the intricate sculpture on the early protoconch both suggest that this species may develop planktotrophically. On the other hand, the small number of larvae (1–6) in capsules from the Juan de Fuca Ridge and the protoconch's large size, inferred value of D/Vol, and unsculptured appearance all suggest that this species has a non-planktotrophic mode of development.

How relatively sedentary organisms at deep-sea hydrothermal vents locate and colonize these geographically isolated environments remains an open question. With the exception of a few preliminary population genetic studies (J. P. Grassle, 1985; Bucklin, 1988), our knowledge of colonization, gene flow and dispersal of organisms between hydrothermal vents has been obtained from inferences drawn from egg capsule type, egg size, fecundity, and larval morphologies retained on adults (Lutz, 1988). Further zoogeographic data and systematic descriptions are needed before we can provide more rigorous answers to questions involving the mechanisms of dispersal and rates of gene flow between isolated areas of deep-sea hydrothermal vent activity. Laboratory culture of these unusual deep-sea molluscan taxa is also necessary to confirm the link between larval shell characteristics and the mode of development. If we assume that the majority of the vent fauna is endemic to the hydrothermal vent habitat [(but see contrasting opinion of Clarke (1986)], and that larval dispersal in non-planktotrophic species is a step-wise process, then each ridge axis should be a discrete dispersal corridor. Given these assumptions, genetic relatedness of the most widely separated non-planktotrophic species' populations along a single ridge axis should be more homogeneous than among populations that are equally separated but belong to two different ridge axes. On the other hand, genetic relatedness of species with planktotrophic development should be more homogenous in the prevailing direction of bottom currents and less reliant on the configuration of ridge systems. The studies of J. P. Grassle (1985) and Bucklin (1988) provide highly paradoxical results. In *Bathymodiolus thermophilus*, a species reported to have a lengthy dispersal stage (Lutz *et al.*, 1980), populations from the Galapagos Rift and 13°N (separated by 2200 km) are genetically distinct. Yet in *Riftia pachyptila*, a non-molluscan species that is believed to have lecithotrophic, demersal larvae with limited dispersal abilities, more widely separated populations from the Galapagos Rift and 21°N along the East Pacific Rise (separated by 3300 km) are genetically similar (Bucklin,

1988). Clearly, an expanded research effort using electrophoretic and molecular techniques to ascertain population structure within species and genetic relatedness among species, coupled with analyses of molluscan larval shell morphology, will be needed to answer questions concerning the rates of gene flow between discrete areas of hydrothermal activity associated with contiguous and non-contiguous oceanic ridge systems, as well as the validity of using larval shell morphology to ascertain dispersal capability in the deep sea.

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